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7. **P. Lambertiana** Doug. Two to six rows of stomata on each face of the triangular section: always two dorsal ducts, often one between, occasionally some ventral ducts which are sometimes parenchymatous, no strengthening cells in fibro-vascular region: leaves 3–4 in. long.

In the Sierra Nevada and Coast Range.

Notes on the mode of pollination of Asclepias.

CHARLES ROBERTSON.

(WITH PLATE VIII.)

In regard to the visitors of Asclepias Cornuti, Dr. Hermann Müller observes that they "slip upon the smooth parts of the flower until a foot enters the wide inferior part of the slit, in which it at last gets a firm hold".[1] Mr. T. H. Corry[2] describes the insect as grasping the back of a nectary, and plunging its proboscis into its cavity, "endeavoring at the same time to get a firm and sure foothold on the unstable flowers", until the insect at length places one of its feet into the wider part of an alar fissure.

Having collected insects on the flowers of six species of Asclepias, I regard the normal action of the most common and most efficient to be that they hold on to a flower, or several flowers, in such a way that their feet go down below the angles of the alæ, and when the legs are drawn upwards they are caught between the strongly projecting hoods and guided by them over the entrance of the stigmatic chamber, which occupies the narrow interval between their bases. Of native insects, the most common visitors I have observed on A. Sullivantii, are humble bees (Bombus separatus, B. Pennsylvanicus, and B. scutellaris) and Danais Archippus. The feet of humble bees reach down as far as the bases of the petals, and I have often found the pollinia fastened upon their tibial spurs as well as on their claws. I have also found pollinia of this species on the spurs and claws of Danais Archippus, and high up on tarsal hairs of Priononyx

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[1] "Befruchtung der Blumen", 1873, p. 336. "The Fertilization of Flowers", translated by D'Arcy W. Thompson, B. A., 1883, p. 398.

[2] "Structure and Development of the Gynostegium and on the Mode of Fertilization in Asclepias Cornuti, Dec.," Trans. Linn. Soc. Lond. Bot. 2d Ser. Vol. II., part 8. 1883, pp. 186, 187.

Thomæ[3]. In a similar way, a specimen of Scolia bicincta shows pollinia of A. Cornuti on the tarsal hairs. However, the gynostegia of these species are so large that the feet of many visitors will not reach far below the angles of the wings, and, when this occurs, the claws are the only parts which are readily caught. The importance of the hoods in guiding the legs of insects over the angles of the wings, is more apparent in the smaller flowered species, since the more delicate wings catch hairs which are not only very fine and short, but which are also situated much higher up on the legs. Thus, hive bees caught on A. Sullivantii and A. Cornuti, show pollinia only on their claws and pulvilli, but they have the pollinia of A. tuberosa, A. incarnata, and A. verticillata scattered upon the hairs of the tarsi. A specimen of Argynnis Cybele, which I caught on A. Cornuti has pollinia of this plant on its claws and pollinia of A. tuberosa on the tarsal hairs. Again, a specimen of Papilio Asterias caught on A. tuberosa has pollinia of A. tuberosa on the hairs of the tarsi and of A. Sullivantii on the claws. Although the pollinia are fastened to different parts, I see no reason for supposing that the action of the insect differs on the different plants. To show how high the pollinia are fastened upon the legs of insects, I may mention that I have found the pollinia of A. incarnata on the hairs of the tibiæ of humble bees 7mm. above the claws, and on Papilio Cresphontes and P. Turnus as high as 9mm. H. Müller gives a figure of the leg of a butterfly showing eleven corpuscula, seven of which are fastened above the claws, four forming a combination on a tibial spur. [4]Dr. A. S. Packard, Jr., figures a Tachytes (?)[5] showing pollinia much as they appear on visitors of the smaller flowered species. In addition to those mentioned above, I have found, among the visitors of A. incarnata, A. verticillata and A. tuberosa, insects of the following genera with pollinia upon the hairs of the tarsi above the claws: Apathus, Melissodes, Ceratina, Magachile, Epeclus, Halictus, Vespa, Polistes, Odynerus, Cerceris, Crabro, Pelopocus, Ammophila, Stizua, Bembex, Astata, Tachytes, Pompilus, Priocnemis, Myzine, Pieris, Colias, Libythea, Conops, Midas, Trichina, and Euphoria. A theory of pollination can not, therefore, be limited to an account of the insertion of pollinia which are attached to the claws; and it is claimed for the view maintained in this paper, that it will account for pollination as readily in the one case as in the other and by the same mode.

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[3] A specimen of Sphex Pennsylvanica in the collection of Prof. S. A. Forbes at Champaign, Ill., has pollinia which I refer to A. Sullivantii similarly situated on its legs.

[4] "Fertilization of Flowers", fig. 133.

[5] Am. Nat , vol. I., p. 105, and "Guide to the Study of Insects", p. 165. Dr. Packard regards the tarsus as that "of a wasp belonging probably" to Tachytes. Mr. W. H. Patton, in Proc. Bost. Soc. Nat. Hist., XX., p. 397, says, "Indeed, that figure bears a resemblance to the tarsus of Tachytes, but represents tolerably well the tarsus of Sphex, an insect of a different family".

H. Müller, who supposes that the whole foot enters the stigmatic chamber, says: "When the insect tries to draw its foot out in order to proceed further, the diverging claws are caught by the apposed edges of the anther-wings, and guided upwards in the slit, so that one or other of the two claws is brought without fail into the notch in the lower border of the corpusculum and there held fast[6]." On the same subject Mr. Corry observes: "When the foot reaches the superior end of the alar chamber in which it has been guided, one at least of the two hooked claws upon it, or some part of the foot in the case of Diptera, must easily enter the hollow cavity of the corpusculum, which lies in such a position that this result is inevitable[7]." The importance which these authors attach to the view that the whole foot enters the chamber, in my opinion, rests on a misunderstanding of the mode of insertion of the pollinia, and has led them to overlook the precision with which a corpusculum comes to be fastened to a hair or claw. The corpusculum is placed so nicely at the top of the wings that its cleft is fairly continuous with the slit between them (fig. 2 *c.*), and I can not conceive that the contrivance works normally unless the particular part, *i. e.*, a single claw, hair, or pulvillus to which the corpusculum becomes attached, is caught between the wings and guided by them into the cleft. Believing that all processes are caught as the leg of the insect passes over the angle of the wing, I suppose that only a single process is caught and that a claw is caught in exactly the same manner as a hair or spur. In a careful examination of the feet of 116 hive-bees which were killed by being caught on the flowers of A. Sullivantii, I have found that, with but two exceptions, when a foot was held by the wings, only one claw was between them, the other being free, or less often the pulvillus was held between the wings and both claws were outside.

When first withdrawn the pollinia lie in the same plane (fig. 4.) In a few minutes the twisting of the retinacula brings the pollinia into nearly parallel planes, but the upper ends are still separated by quite an interval (fig. 5.) According to the authors to whom reference has been made, the pollinia are inserted by the corpusculum. From the analogy of observations made on the movements of the pollinia of some Orchidaceæ some advantage might be looked for in the slow movement of the pollinia of Asclepias. Indeed, Mr. Corry, who has observed this phenomenon in A. Cornuti, states that it is of advantage, although he fails to show it; and I think it impossible so to do on the supposition that the pollinia are introduced by the corpuscula. He says: "Some considerable time, moreover, must elapse after the pollinia are extracted before the corpuscular appendages are so far dried that both pollinia of the same corpusculum can be introduced through the fissure into the alar chamber, and in the meantime the insect has had time to reach another flower or plant[8]." On another page he observes: "If the movement did not occur on the part of the pollinia their broad surfaces would lie at right angles to the alar fissure, and their insertion into it in this position through the notch would in consequence be rendered a much more difficult, if not an altogether impossible operation; or else the pollinia in being slipped in would become folded in the opposite direction, and the less curved border which emits no pollen tubes would be first inserted into the fissure[9]." But what is to prevent this consequence before the movement takes place? Whatever might happen there is obviously nothing to render the introduction of the corpusculum itself more difficult before the movement occurs than afterwards, so that the slowness of the movement is hardly an advantage under this view. If the corpusculum were very slender or flattened so that a thin edge could be presented to the slits, there would be no difficulty in understanding how it could readily slip into the stigmatic chamber; but it is a rounded body, and is relatively large in comparison with the entrance to·the cavity. Of course, if the whole foot of an insect commonly enters the stigmatic chamber it is not hard to understand how the corpusculum should go in with it. But when the corpusculum is fastened to a hair which is directed outward and downward from the leg of the insect, and which is often so short that the corpusculum is fairly in contact with the leg, the difficulty increases. In the examination of the feet of hive bees killed on the flowers, I have failed to find a single case in which a corpusculum was attached to that part of the foot which was held between the anther wings. In my opinion, therefore, the structure of the corpusculum is so far from facilitating the introduction of the pollinia that it prevents the part to which it is attached from being again caught in the slits; and, until the movement occurs, the corpusculum with its two pollinia will pass over the entrance to the stigmatic chamber without being injured.

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[6] Ibid, p. 398.

[7] Ibid, p. 188.

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[8] Ibid. p. 195.

[9] Ibid, p. 190.

After the movement occurs, if the corpusculum be examined from one side (fig. 6), it will be observed that the retinacula project outward and downward. Since the parts to which the corpuscula are attached themselves project outward and downward, the retinacula finally stand nearly at right angles to the leg of the insect. The retinaculum, near the point where it joins the pollinium, is bent rather suddenly, so that the pollinium appears to be flexed upon it. This flexure, which Mr. W. H. Leggett[10] has called the knee, is very prominent. There is quite an interval between the knees, and the membrane of the retinaculum at the knee is expanded transversly to the plane of the pollinium (fig. 5 *k.*) Robert Brown[11] has observed in A. purpurascens, that the part of the retinaculum extending between the knee and the pollinium remains attached to the latter when it is found in the stigmatic chamber. This expansion of the membrane serves to prevent the withdrawal of the pollinium after it has been inserted into the cavity, and, when drawn against the closely apposed edges of the alæ in the upper part of the stigmatic chamber, facilitates the rupture of the retinaculum. Judging from the structure of parts which are readily caught between the anther-wings, nothing could be more natural than for one of the knees to slip into the entrance to the stigmatic chamber, and the movement is intended to turn them into such a position that this will occur. When, therefore, the movement has taken place and the insect draws its leg over the angle of the wings, the corpusculum with the claw or hair to which it is attached passes on without being caught, while one of the knees of the pollinia readily enters the stigmatic chamber and the pollinium enters with it. When the knee has reached the upper part of the cavity and will go no further, the retinaculum is torn across and escapes, leaving the pollinium in position to effect fertilization.

In repeated trials at artificial pollination of the flowers of A. Cornuti, A. Sullivantii, and A. incarnata, I succeeded three times, in the case of A. Sullivantii, in separating the pollinium from the retinaculum without withdrawing the latter from the slit, and thus was enabled to insert a pollinium and to draw out a corpusculum at the top of the alæ with its two pollinia by the same movement. But in all other cases a pull that seemed sufficient to break the rectinaculum freed it from the slit so that the corpusculum at the top remained intact. Accordingly, I have seen no difficulty, on the supposition that the pollinia are introduced by the knees, in the observation of H. Müller, who says: "In several flowers which I dissected the corpuscula and pollen masses were still in their places, though pollinia, which must have come from other flowers, had been inserted into the stigmatic chambers[12]."

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[10] Bull Torr. Bot. Club, Vol. III, p. 35.

[11] Trans. Linn. Soc. Lond., Vol. XVI, p. 724.

In a number of cases observed by me on A. Sullivantii the movement which turns the knees toward the flower is completed in about seven minutes, though it has proceeded sufficiently in five minutes to turn the flexure far enough to render its insertion quite likely. With the view of pollination stated in this paper, the slow movement is plainly of advantage, because a knee can hardly be caught by the wings until it has occurred.

Now, since only one pollinium is inserted into the stigmatic chamber, there is an economic disposal of the pollinia. The interval between the flexures is so great that only one of them can be caught, while the other passes by the slit uninjured. There are, therefore, two chances of a pollinium being transferred to another plant. If both pollinia were left at each act of pollination, there would be but one chance of cross fertilization. Moreover, the chances of cross fertilization would be reduced from the fact that the stigmatic chambers would be more nearly filled by pollinia from the same source, while if they are introduced singly, there are more chances of a chamber receiving a pollinium from a distinct plant.

As two pollinia are fastened together, there would be but one chance of pollination occurring if the pollinia were inserted by the corpuscula, while there are two chances of a knee being caught. When a pollinium has been removed, the broken retinaculum may be caught in a slit and remove a second corpusculum with its two pollinia. When this combination of two corpuscula and three pollinia is drawn over the angle of the wings, there are three chances of a pollinium being caught. Whenever a pollinium is removed, two new pollinia may be substituted for it and a large combination of pollinia may result, arranged either in a unilateral series or dichotomously. In either case, the chances of the insertion of a pollinium equals the number of pollinia in the combination. If the foot to which the first corpusculum of the combination is attached must enter the stigmatic chamber, of course, there would be but one chance of pollination taking place without regard to the number of pollinia. Such an accident would be likely to destroy the whole combination. As already observed, on the large flowers of A. Sullivantii and A.

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[12] Ibid, p. 400.

Cornuti the shorter hairs on the legs of insects are not readily caught, so that the number of parts to which the corpuscula may be attached are reduced to a minimum. For instance, the only parts on the leg of a hive bee which can remove the corpuscula of these species are the two claws and the pulvillus. The leg will thus remove three corpuscula, and since these bodies render useless the parts to which they are attached, the broken retinacula not only take the place of the parts disqualified, but increase the number of parts to which the corpuscula can be attached. By means of these combinations, therefore, the leg of an insect has its capacity for carrying pollinia greatly increased.

Mr. Corry, referring to the simplest form of combination, viz., two corpuscula and three pollinia, says: "This combination being inserted into the alar fissure, as the single corpusculum was previously, one of the two lower pollinia is left detached in the lower part of the chamber, while its appendage, becoming caught at the upper part in the fissure of the corpusculum which lies there, carries it away, forming a combination of three corpuscula and four pollinia[13]." This suggests a most serious objection to the view that the pollinia are introduced by the corpuscula. It makes a mystery of the mode of retention of the pollinia, for how are we to understand how one pollinium is retained after the foot with two corpuscula and two pollinia have escaped. However, so long as the combination remains uniserial, Mr. Corry finds no difficulty in its passage through the stigmatic chamber; but when it becomes dichotomous the difficulty becomes insurmountable, and, to account for this form, he makes use of the theory which I have applied throughout. He says: "These corpuscular combinations are, however, frequently more or less regularly dichotomous in their arrangement, and this can only occur by one of the projecting corpuscular appendages, either with or without a pollinium attached to it, becoming caught in the open lower extremity of an alar chamber; it is then drawn upwards in the cavity, its pollinium, if it has one, is usually detached in the lower part, and then in any case the appendage simply passes upwards as the insect raises its leg and lifts out the corpusculum situated at the apex of the chamber, along with its pair of appended pollinia. I am unable to conceive that this dichotomous form can be brought about in any other way, since the alar chamber is in all cases of much too contracted dimensions to admit of the passage of any form of combination except a unilateral series such as that previously mentioned, *i. e.*, a combination with a single pollinium directly attached to each corpusculum save the last, which has two pollinia[14]." This is a plain admission that the view that the pollinia are inserted by the corpuscula will not account for the formation of dichotomous combinations of pollinia, and involves the whole theory of the insertion of pollinia by the corpuscula. For if a pollinium in a dichotomous combination can be inserted by the knee, any other pollinium may be inserted in the same way, and the theory of insertion by the knee may be applied throughout without meeting any difficulty. The supposition that the pollinia are inserted by the knees explains the formation of these as well as of unilateral ones, and shows the value of both forms; for the combination becomes the equivalent of a leg provided with a number of pollinia, each one of which may be inserted separately.

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[13] Ibid. 191.

Finally, I have seen the pollinia of A. Sullivantii introduced into the stigmatic chambers in the manner above described. The pollinia and the entrance to the chamber in this species are very large and are easily seen, and hive bees move so slowly in effecting pollination that, after a knee is caught, one can see the pollinium slowly disappear between the wings, so that there can be no doubt as to the manner of insertion. Commonly, however, the insertion of pollinia occurs so rapidly that it is impossible to see how it really happens. After a pollinium has been introduced into the chamber, hive bees always have difficulty in breaking the retinaculum, and they lose their lives on account of this as well as on account of the difficulty in drawing their claws through the slit. When a foot is held by a retinaculum the pollinium is found in the chamber, with every indication that it was introduced by the knee.

EXPLANATION OF FIGURES ON PLATE VIII.—1. Flower of *A. Sullivantii* Engelm (sepals and petals removed). 2. Anther wings of same. 3. Stigmatic chamber. 4. Pollinia when first withdrawn. 5. Same after twisting of retinacula. 6. Same, seen from the side.

a. anther wing. *c.* corpusculum. *e.* entrance to stigmatic chamber. *k.* knee. *r.* retinaculum. *s.* stigmatic chamber. *p.* pollinium.

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[14] Ibid. pp. 191, 192.